Overestimation of force during matching of externally generated forces

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Non-technical summary If a weight is applied to a finger and the subject asked to produce the same force, the subject generates a force larger than the weight. That is, subjects overestimate the force applied by an external target when matching it. Details of this force overestimation are not well understood. We show that subjects overestimate small target weights, but not larger ones. Furthermore we show for the first time that the force overestimation consists of two components. The first component is a constant. The second component depends on the precise magnitude of the weight and is only present when subjects hold the target weight against gravity. We suggest that the two components are generated in different phases of the force-matching task, are due to different processes, and must have an influence on all proprioceptive judgements of force.

Abstract To make accurate movements the brain must differentiate between forces it commands and forces imposed by the environment. This requires afferent information and signals related to central commands. If subjects match an externally generated target force with a self-generated force, they produce a force that is larger than the target. It has been proposed that this is due to simple attenuation of afferent force signals produced by the body's own actions, but the mechanisms are unclear. Four studies of forces applied to the index finger in 14 subjects investigated this force overestimation. We determined which sensory signals are involved, if handedness is important, if overestimation is present at high forces, and which muscle actions can generate it. Subjects overestimate an externally generated target force by 2–3 N when matching it with a voluntary force using a simple contraction or complex muscle synergy. This 'offset' occurs at low but not high forces. The effect occurs when only cutaneous inputs, or when only combined inputs from muscle and central command sources can signal force. We report a novel central factor that increases the gain, or gradient of the relationship, between the matching and target forces to ∼1.20. This increased gain is present only if the target force is received on an active finger and persists after the 'offset' is abolished. It may reflect processing of reactive forces during the target phase of the task. Overall, the previously described simple model of force attenuation cannot explain fully the overestimation of external forces.

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Introduction

Both exteroceptive and proprioceptive senses are important for our interaction with the environment as we must know both how the environment acts on our body and how our body acts on the environment and itself. We perceive how hard our muscles work to perform a task as well as how much force is produced. Forces are detected by afferent information, which comes from tendon organs, signalling the contractile forces of the muscles and skin receptors which signal skin compression. Central information related to the amount of central motor command also provides information about how much the muscle has been activated. This can signal muscle force (e.g. McCloskey *et al.* 1974; Gandevia & McCloskey, 1977; Gandevia, 1996; Carson *et al.* 2002), limb movement (Walsh *et al.* 2010) and position (Walsh *et al.* 2004; Gandevia *et al.* 2006; Walsh *et al.* 2009). These central signals may also correct for reafferent sensory 'noise' (Goodwin *et al.* 1972; Bays & Wolpert, 2007). A reafferent signal (or reafferance) refers to sensory input produced by the body's own actions, as opposed to an exafferent signal (or exafference) which is sensory input generated by external factors.

If a weight sits on the hand resting on the table, then only skin information is available. Once muscles contract to hold the weight, additional information is available from tendon organs and motor command signals. If subjects are asked to match an external force they produce a larger self-generated force (Shergill *et al.* 2003, 2005; Voss *et al.* 2007). The proposed reason is that the nervous system attenuates the feedback from self-generated forces to reduce the 'noise' of our own actions, making us more sensitive to externally generated forces. Various mechanisms have been proposed over the years to correct or remove reafferent signals . The original models focused on visual localisation and kinaesthesia of the eye (Sperry, 1950; von Holst, 1954). Since then the subtraction of reafferent signals has been shown for other sensory systems including the electric sense of electric fish (Bell, 1982), and the vestibular system (Roy & Cullen, 2001; Cullen *et al.* 2009). This mechanism has also been frequently tested in the somatic domain with cutaneous stimuli (Weiskrantz *et al.* 1971; Dyhre-Poulsen, 1975; Coquery, 1978; Angel & Malenka, 1982; Starr & Cohen, 1985; Milne *et al.* 1988; Jiang *et al.* 1990; Blakemore *et al.* 1998; Williams *et al.* 1998). Most of these studies have focused on the detection and perceived intensity of electrical stimuli applied to the skin, rather than more natural stimuli, such as compression of the skin when an object is touched. Furthermore, the other somatic signals, such as those from muscle receptors, have not received the same attention.

A model has recently been proposed for the attenuation of self-generated forces (Bays & Wolpert, 2007), but details of the mechanism have not been investigated. It is unclear whether the overestimation manifests as a constant force 'offset' (Shergill *et al.* 2005; Voss *et al.* 2007) or whether it includes a 'gradient' (Shergill *et al.* 2003). It has also been reported that when the target force is received on an active finger the results do not significantly differ from the passive condition (Shergill *et al.* 2003). However the details of the overestimation effect under these active conditions, when signals from muscle receptors and central sources are available, are unknown. This study consisted of four experiments on matching forces applied to the index finger. The first investigated which sensory signals are involved when subjects overestimate during force matching. The second examined whether the hand to which the target force was applied made a difference. The third compared two different matching actions and also self-generated forces. Because the overestimation effect has only been investigated for small forces, and because subjects cannot produce a larger matching force as they approach their maximum, the fourth experiment tested a wide range of forces.

Methods

Fourteen healthy subjects (four male) aged 27–39 participated in this study. Two (female) participated in all parts, six (two male) participated in the first three experiments and the other six (two male) participated in the fourth experiment. All subjects gave written informed consent and the experimental procedures were carried out in accordance with the *Declaration of Helsinki*. The University of New South Wales Human Research Ethics Committee approved the study. The subjects were informed about the experimental procedures, that is, that they would perform weight matching tasks with their index fingers under various conditions, which were also explained. However the subjects were kept unaware of the precise experimental hypotheses.

Experimental set-up

Figure 1 depicts the experimental set-up. The test arm, left or right depending upon the experiment, rested supine on a table supported under the forearm from the elbow to the wrist with the back of the hand unsupported. The index finger was held extended with a load cell that was attached to a shaft suspended over the distal segment. The load cell was free to move up and down, or it could be locked into position. The subject was instructed to keep the remaining fingers in a relaxed, slightly flexed position. A support was placed under the index finger if the experiment required a passive test finger. If an active test finger was required the finger support was removed and the subject was instructed to hold their finger in position. When the target force was externally generated, weights were placed on the platform located on top of the load cell shaft. If the target force was to be self-applied, then the subject pushed down on this platform with their contralateral hand. Using the contralateral hand here allowed the index finger receiving the force to remain passive if necessary. This was also the way that subjects produced a matching force with the contralateral hand when required. If the match was to be generated with the test index finger, then the shaft was locked and the subject flexed the index finger isometrically against the load cell. The subjects were denied vision of their index finger, their contralateral hand and the apparatus.

Experiment 1. Force matching with the index finger passive, active, or active with a digital nerve block

The purpose of this experiment was to investigate the performance of a force-matching task under conditions in which different sensory information was available. The first condition, *index passive*, used a passive test finger so that only information from skin receptors was available. This is similar to previous studies (Shergill *et al.* 2003). The second condition, called *index active*, used an active finger so that information from skin receptors, muscle receptors and central command signals were available. The third condition used an active test finger with its digital nerves blocked by an injection of local anaesthetic. This is referred to as *index active with digital block*. Under this condition information from muscle receptors and central command signals was available but information from skin and joint receptors in the finger was not. For all three conditions the target force was externally applied with weights on top of the load cell platform (Fig. 1) and the subject matched by pushing down on the platform with their contralateral hand. For each of the three conditions 10 different forces were presented, ranging from 1 N to 10 N in 1 N increments. Ten newtons is approximately 25% of the maximum voluntary force that can be generated by the finger. Each force was presented five times (total 50 trials) and the order of trials was randomised. Each of the three conditions was tested in a block of 50 trials, in the order of *index passive*, *index active* then *index active with digital block*.

For each trial, weight was placed on the subject's finger via the load cell and the experimenter said, 'Here is a force'. The subject was given ∼3 s to judge the force before the weight was removed. Next, the subject was told, 'Apply the same force with your other hand', and the subject used their contralateral hand to push down on the platform to match the force on their index finger. The subject began to generate the matching force within 2 s of the target force being removed. In the two conditions *index active* and *index active with digital block* the subjects were required to maintain the position of their index finger. They were instructed to hold the position of their finger at the start of the condition as the weight was lowered onto it. This instruction was given for all conditions in which the index finger was active to support the weight.

Blocking the digital nerves of the index finger. A total of 3–4 ml of 1% lignocaine was injected into the medial and lateral side of the index finger 10 mm distal to the metacarpal joint to block both digital nerves. A band was placed around the index finger just distal to the joint to impede slightly the venous return in the finger and thus prolong the block. The block was clinically complete in 5–10 min with complete loss of light touch sensation. Light touch was tested intermittently to ensure that the block remained complete. After the experiment the band around the finger was removed and the subject recovered completely within a few hours.

Experiment 2. Force matching with different hands

This experiment was performed to test for an influence of handedness on the overestimation effect seen in the results of Experiment 1 and so the experimental procedure was similar. There were two conditions, *index passive* and *index active*. The order of events within a trial was the same as for Experiment 1. The target force was always

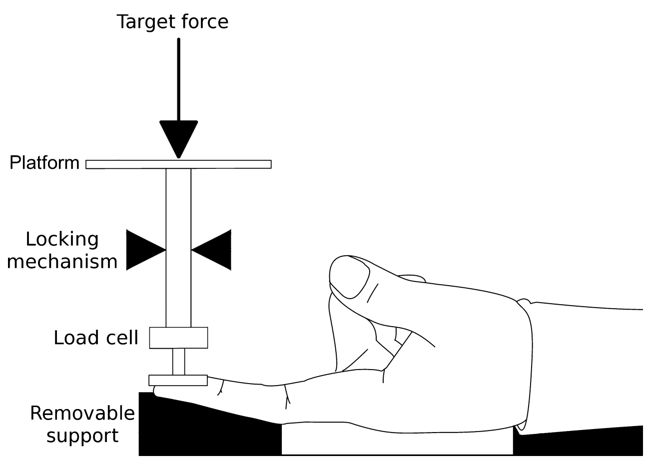

Figure 1. Diagram of the experimental set-up
The subject's forearm rested on a table with the hand protruding off the edge. During experiments in which the subject's index finger was required to be passive, it rested on a support, but in experiments in which subjects were required to actively hold the index finger in position the support was removed. The shaft of the load cell could be locked in place or free to move up and down. The initial target force was produced by an external force on the index finger or by a self-generated force made by the contralateral hand (see Methods). The initial target was applied for ∼3 s. The subject was asked to generate the matching force either by pushing down on the top of the platform with the contralateral hand while the shaft was free to move or by pushing up isometrically against the load cell with their index finger while the shaft was locked.

externally applied by placing weights on the platform and the subject always matched by pushing down on the platform with their contralateral hand. Once again forces ranged from 1 N to 10 N in 1 N increments and were used in randomised 50-trial blocks. However, in this experiment, both conditions were presented to the index fingers of both hands, creating a total of four blocks of trials. The order in which the blocks were presented to subjects was varied. The conduct of each trial and instruction to the subject were the same as for Experiment 1.

Experiment 3. Force matching with a self-generated target *vs*. an externally generated target

In the previous two experiments all matching forces were generated by the subjects via a complex multi-joint movement with their contralateral hand pushing down on the load cell platform to generate a force on their test index finger (Fig. 1). In the third experiment matching forces were generated by the subject simply pushing back on the load cell with their test index finger, after the shaft of the load cell was locked in place. The first purpose of this experiment was to determine if there was any difference in force matching with the 'push-back' matching compared to matching with the contralateral hand used in Experiments 1 and 2. The second purpose was to test if the overestimation of force observed in the experiments persisted when the subject was responsible for generating both the target force and the matching force.

This experiment had four different conditions. In the first (*target external, index passive*) the target force was generated by placing weights on the load cell platform as for the previous experiments. As before, the target force was applied to the pad of the index finger with the instruction, 'Here is a force', and the subject was given ∼3 s to assess the force before it was removed. After the target force was removed the load cell was locked just above the subject's index finger. Then the subject was asked to, 'Apply the same force by pushing back', and the subject flexed isometrically against the load cell to generate the matching force. This first condition (*target external, index passive*) was performed with the index finger supported and passive. The second condition (*target external, index active*) was the same except that the finger was unsupported and active during the presentation of the target force. The third condition (*target self-applied, index passive*) used a passive finger and the target force was generated by the subject, as follows. On an oscilloscope, the subject received visual feedback of the force applied to the load cell with a line that corresponded to the target force for the trial. The subject was asked to push down on the load cell platform with their contralateral hand to the target force with the words, 'Use your other hand to push to the line.' The subject held the target force for ∼3 s before being told to relax. Then the visual feedback was removed, the load cell was locked into position and the subject was told, 'Apply the same force by pushing back', and the subject flexed with the index finger to produce the matching force. So both the target force and the matching force were voluntarily controlled by the subject. The fourth condition (*target self-applied, index active*) was as for condition 3 except with an unsupported active finger. For this experiment four target forces were used ranging from 2.5 N to 10 N in increments of 2.5 N and each force was presented five times making a total of 20 trials for each condition. The order of trials for a condition was randomised and the order of conditions varied.

Experiment 4. Force matching at high forces

The fourth experiment was designed to determine whether the force matching overestimation effect was abolished at forces that were a large percentage of the subject's maximal voluntary contraction (MVC). It is expected that subjects cannot continue to overestimate the target force as it approaches the maximum force available from the index finger. Finger flexion MVC was measured three times and the largest was taken as the subject's maximum. During each attempt subjects received verbal encouragement and were provided with visual feedback of their force. Subsequently, four levels of force were used, 15%, 35%, 55% and 75% of the subject's MVC and each was presented five times (total 20 trials) in each of the three conditions. In all conditions the target force was applied using weights placed onto the load cell platform. In the first condition the index finger was supported and passive, and the matching force was generated by the subject's contralateral hand pushing down on the load cell platform. The second condition also used a passive index finger but the matching force was generated by the subject pushing back against the load cell that was locked into position. The third condition was the same as the second but the index finger was unsupported and active. The order of trials within a condition was randomised and the order of the three conditions varied. Because of the higher forces used in this experiment subjects were given longer rests between trials to ensure that no fatigue occurred.

Data collection, analysis and statistical methods

The signal from the load cell was amplified and then digitised at 100 Hz by a CED 1401 (Cambridge Electronic Design, Cambridge, UK) and recorded with CED Spike2 v6 software. Target forces were measured as a mean force over the presentation, except in trials where the index finger was active and the target was applied with weights. Here the first 0.5 s was excluded to allow time for the subject to steady the weight. The matching forces were measured as the maximum force the subject applied during the match. Subjects had been instructed to increase their applied force until it reached the desired matching force. Data from Experiments 1, 2 and 3 underwent regression analysis to determine the equation for the line of best fit and the statistical significance of that line. Threshold for significance was set at $P < 0.05$. Data from Experiment 4 were pooled into four groups, each corresponding to one of the four target forces. Ninety-five per cent confidence intervals were calculated for both the target and matched forces. Mean data and the gradients and y-intercepts of lines of best fit are reported as means ± 95% confidence intervals.

Results

In Experiment 1 we determined the ability of subjects to match an externally applied force to their index finger under three conditions in which different sensory information was available from the test finger. Subjects overestimated external forces applied to their finger when they produced a voluntary matching force. We then performed three further experiments to investigate this overestimation in more detail.

Experiment 1. Force matching with the index finger passive, active or active with a digital nerve block

The target force was applied externally by placing weights on the target finger and the subject generated the matching force with the contralateral hand by pushing down on the weight platform. Subjects overestimated the external target force when matching it with a self-generated force in all three conditions. In the *index passive* condition the index finger was supported and remained relaxed so that only information from the skin was available to signal the force. Data from one subject performing this task are shown in Fig. 2. The subject consistently produced a matching force that was larger than the target force. However, the amount by which the subject overestimated the force did not depend on the target force. There was no change in the gradient of the data away from unity. Similarly, the mean data for the group (Fig. 3*A*) also showed a gradient not different from 1 (1.05 [0.92, 1.18], mean [95% CI]) but a y-intercept of 2.13 N [1.38 N, 2.88 N]. When information from skin receptors was removed by local anaesthesia but information from muscle receptors and central signals was present (Fig. 3*C*), there were similar findings, with a gradient of 1.11 [1.0, 1.22] and a y-intercept of 2.53 N [1.88 N, 3.18 N]. In the *index active* case (Fig. 3*B*) the gradient of the data was greater than 1 (1.27 [1.17, 1.37]) but was not different from the other two conditions in this experiment. The y-intercept of the line of best fit was 1.82 N [1.21 N, 2.43 N]. The y-intercepts and gradients for each condition are summarised in Fig. 4.

Experiment 2. Force matching with different hands

Experiment 2 tested if the overestimation effect observed in Experiment 1 was the same whether subjects used the left or right hand. All subjects were right handed. Results for Experiment 2 were similar to the data from Experiment 1 (Fig. 4, Experiment 1 and 2). Again there was a positive y-intercept for the line of best fit through the pooled data, 3.04 N [2.36 N, 3.72 N] for the *left index passive* condition, 2.51 N [1.96 N, 3.06 N] for *right index passive*, 2.82 N [2.24 N, 3.40 N] for *left index active*, and 2.36 N [1.81 N, 2.91 N] for *right index active* (Fig. 4, upper panel). For the two passive conditions the gradient of the line of best fit for the pooled data was not different from unity (left: 0.95 [0.88, 1.02]; right: 1.03 [0.98, 1.08]; Fig. 4, lower panel). For the two active conditions the gradients were 1.15 [1.09, 1.21] and 1.19 [1.13, 1.25] for *left index active* and *right index active*, respectively. Unlike Experiment 1, the gradients of the data for the active conditions were different from the gradients of the passive conditions in addition to being greater than 1. The overestimation seen

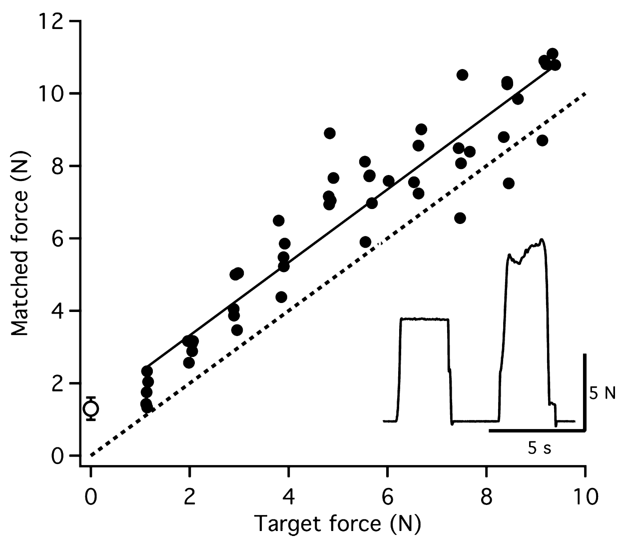

Figure 2. Data from a single subject during a *target external, index passive, match contralateral* task experiment
An external target force was applied to the subject's passive index finger by a weight for ∼3 s. After it was removed the subject matched it by generating a force on the index finger by pushing down with their contralateral hand. There is a significant ($P < 0.001$) linear relation between their matching force and the target force applied to their index finger. This subject consistently applied a matching force that is higher than the target force. The data are offset (open circle [95% CI]) above the line of identity (dashed line) but still have a unity gradient. The inset shows raw data from one trial. The first increase in force is the external target and the second is the matching force produced by the subject with the contralateral hand.

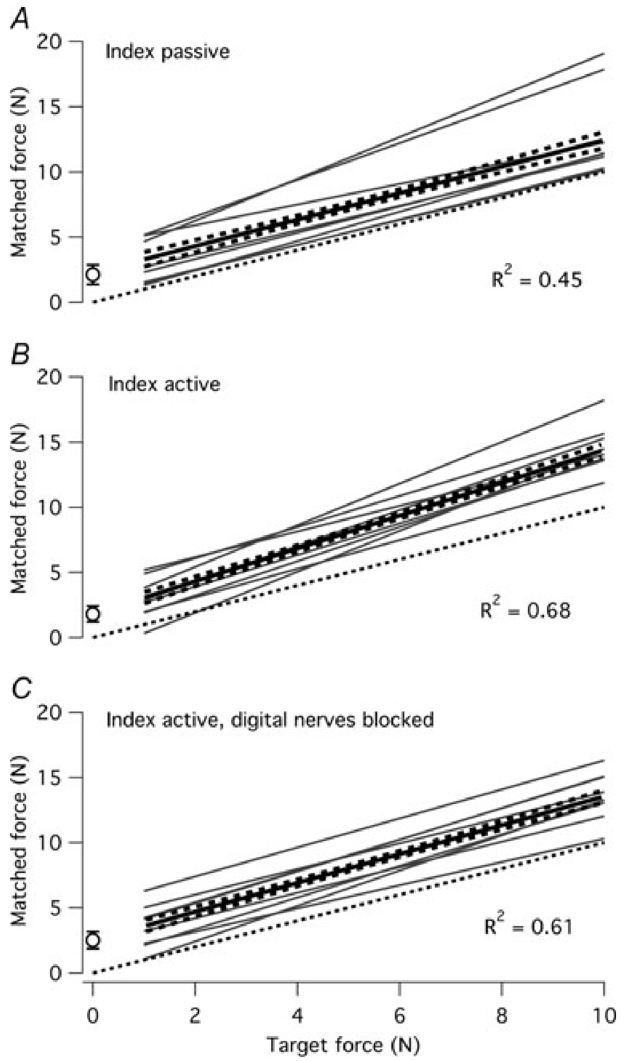

Figure 3. Group data from Experiment 1 (8 subjects) for *target external, match contralateral* tasks
Thick lines are the line of best fit for the pooled data shown with a 95% CI (dashed lines). The grey thin lines are lines of best fit for data from individual subjects. For all three panels the target force was applied externally with a weight onto the index finger and the subject produced a matching force with the contralateral hand. *A* shows data from a task in which the index finger was passive and rested on a support. In *B* the index finger was actively held in position by the subject. *C* is the same task as for panel *B* with the index finger being actively held in position by the subject, but its digital nerves had been blocked with local anaesthetic. The results are similar for all three conditions. On average, subjects consistently apply a matching force that is greater than the target force. The relation between the matching and target forces is linear for all three conditions ($P < 0.001$). The data from all three tasks show a positive *y*-intercept (~2 N, open circles). The gradient for the linear relation in the index passive task (1.05 [0.92, 1.18], mean [95% CI]) and the index active, digital nerves blocked (1.11 [1.00, 1.22]) are not different from unity. The gradient for the index active task is 1.27 [1.17, 2.31]. It is not different from the gradients of the other two tasks.

here and in Experiment 1 did not depend on whether forces were applied to the left or right index finger (or whether matching forces were produced by the left or right hand).

Experiment 3. Force matching with a self-generated target *vs.* an externally generated target

Two subjects were unable to perform the two tasks that required a passive index finger. They found these tasks too difficult and hence their data were excluded. In this experiment the matching force was generated by the subject pushing back against the load cell with the test index finger, rather than the contralateral hand as in the previous experiments. In addition there were two target conditions, either the target was externally generated with weights, or self-generated by the subject. When the target force was externally generated (Fig. 4, Experiment 3) the results were consistent with data from Experiments 1 and 2. That is, subjects matched with a force that was larger than the target force and the data were offset above the line of identity by 2.19 N [0.83 N, 3.55 N] for the *target external, index passive* condition and 1.50 N [0.77 N, 2.23 N] for the *target external, index active* condition. Once again, the gradient of the data for the passive finger was not different from unity (0.94 [0.68, 1.20]). While the gradient for the active data was greater than 1 (1.17 [1.02, 1.32]), it was not different from that for the passive condition. When the subjects matched a self-generated target force they were able to do so more accurately and the pooled data were located around the line of identity (Fig. 4, broken box). The offsets for the *target self-applied, index passive* task (0.22 N [−0.87 N, 1.31 N]) and the *target self-applied, index active* task (−0.88 [−1.77, 0.01]) were not different from zero. The gradients of the pooled data for these two tasks were not equal to 1 with the *target self-applied, index passive* gradient being <1 (0.74 [0.60, 0.88]) and the *target self-applied, index active* gradient >1 (1.17 [1.05, 1.29]). These two gradients also differed from each other.

Experiment 4. Force matching at high forces

The fourth experiment tested the force matching performance of subjects over a wide range of forces from 15% of maximal voluntary contraction (MVC) of index finger flexion up to 75% MVC. The mean MVC was 41.2 N [37.0 N, 45.4 N]. The target force was always applied externally with weights but the matching force was generated with either the contralateral hand or the test index finger. For the *index passive, match contralateral* task an overestimation effect was observed at forces up to ~55% MVC (Fig. 5*A*). During the *index passive, match index-flexion* task, subjects overestimated target forces of 15% MVC and matched accurately a target force of 35%

MVC (Fig. 5*B*). However when the target force was 55% or 75% it was matched with a force that was *smaller*. For the *index active, match index-flexion* condition the subjects matched with a larger force for targets of 15% and 35% MVC, but otherwise were accurate in their matching (Fig. 5*C*).

Discussion

Subjects overestimate an externally generated target force when matching it with a self-generated force, a finding consistent with previous reports (Shergill *et al.* 2003, 2005; Voss *et al.* 2007). However, the cause of this overestimation is not as simple as the attenuation of sensory reafference that has been suggested (Bays & Wolpert 2007). Our novel findings are that this overestimation effect occurs consistently under several conditions at low forces including when we restrict which sensory signals can contribute, but it does not occur consistently at high forces. In addition, there are two components to the overestimation, a constant component (i.e. offset) and one that depends upon the level of force (i.e. a gradient or

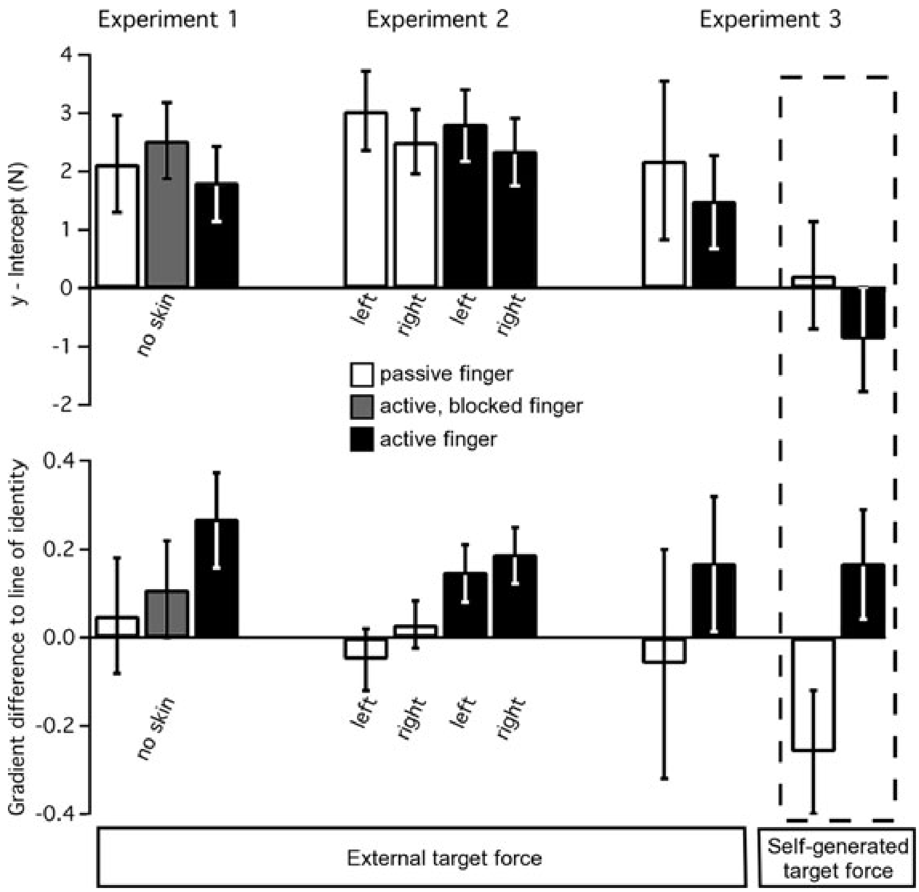

Figure 4. The mean *y*-intercepts and gradients of the overestimation for each condition from Experiments 1, 2 and 3
The upper panel shows the size of the offset component (±95% confidence interval) which was determined from the *y*-intercept of the mean line of best fit between matching force and target force for each condition in each of the experiments. The lower panel shows the size of the gradient component of the overestimation as a difference (± 95% CI) between the gradient of the mean line of best fit and the line of identity (i.e. observed gradient minus 1). The test finger was either passive (white columns) or active (filled columns). In Experiment 1, the test finger was anaesthetised in one condition (grey column, no skin). In Experiment 2, the test finger was the left or right index in different conditions. In Experiments 1 and 2, subjects used the contralateral hand to push on the force transducer to produce the matching force on the test finger. In Experiment 3, subjects produced the matching force by pushing back on the transducer with the test finger. In Experiments 1 and 2 and in two conditions in Experiment 3, the target force was externally generated by weights. In the other two conditions of Experiment 3 (dashed box), the target force was self-generated by the contralateral hand. An offset of 1.5–3 N is present when the subjects match an externally generated target force, but is abolished when the subjects generate the target force themselves (dashed box). A gradient steeper than the line of identity is only present when the subject is required to actively maintain the position of the index finger when the target force is presented (filled columns). Gradients shown here as 0.15–0.25 more than the line of identity represent total gradients of 1.15–1.25.

gain). This separation has not been described before and it appears that previous studies focused on the constant component, as the gain component is only present in some studies (e.g. Shergill *et al.* 2003, 2005).

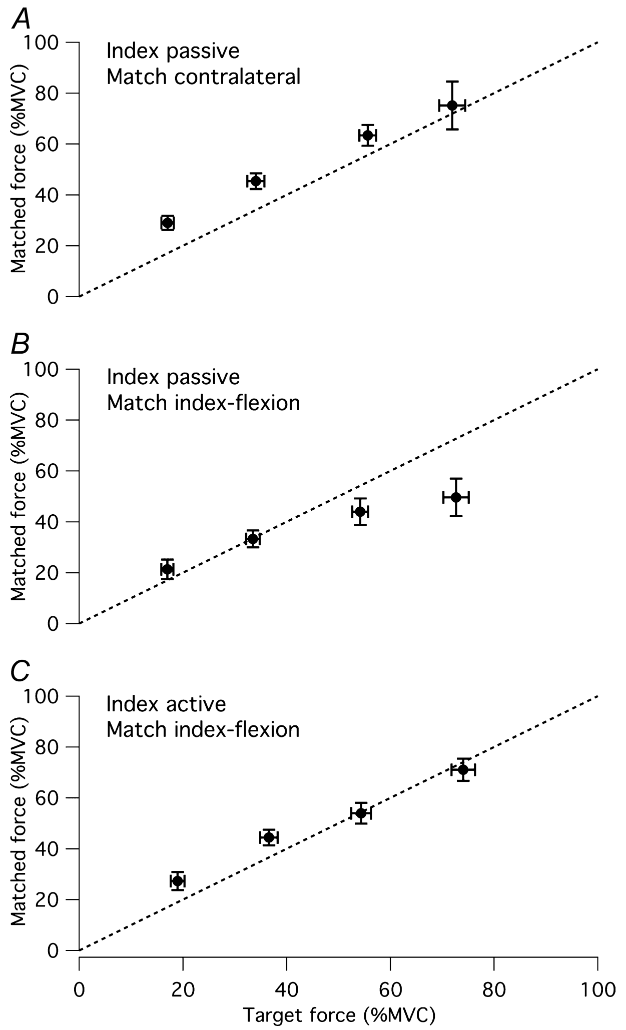

Figure 5. Pooled data from Experiment 4 (8 subjects) for target forces that are 15–75% maximum voluntary contraction (MVC)
In all panels the target force was externally applied with a weight. Data are shown as means ± 95% confidence intervals. In *A* the index is passive and the matching force is self-applied with the contralateral hand. Here subjects matched with a higher force than the target for all forces except for 75% MVC. *B* shows the data obtained when the index was passive and supported when the target force was applied and the matching force was generated by flexing the index finger against the load cell, which had been locked in position. On average, subjects match with too high a force only at 15% MVC. At higher forces subjects match accurately (35% MVC) or match with a force that is lower than the target force (55% MVC and 75% MVC). *C* is a task in which the subject actively holds the index finger in position and the matching force generated by flexion of the index finger against the locked load cell. In this task subjects, on average, matched with a force that was higher than the target for forces less than 50% MVC but accurately matched forces that were greater than 50% MVC.

Our findings for the constant component of the force overestimation effect are consistent with previous findings. Apart from two conditions in Experiment 3, all conditions involved a subject matching an externally generated force with a self-generated force. When subjects did this, they consistently overestimated the target force by 2–3 N, shown as a positive y-intercept with matching force plotted versus target force. This offset is larger than previously reported (e.g. Shergill *et al.* 2003) but is still abolished when both the target and the matching force were self generated. Furthermore, subjects overestimated their target when force information was available only from skin receptors, only from muscle receptors and central signals, and when all sources were available. Thus, this overestimation is not restricted to one sensory channel and includes somatic signals beyond the cutaneous signals that have been the focus of previous study on sensory attenuation. We found no effect of handedness, suggesting that the effect is not linked to any discrepancy between the sensory or motor abilities of the dominant and non-dominant hands. It was important to assess the effect of handedness because manual performance with the index finger differs with hand dominance (Brouwer *et al.* 2001).

In our first two experiments, the subjects received the target force on their index finger but produced the matching force with their contralateral hand. In the third experiment, subjects produced the matching force with the same finger that received the target force. Pushing back with the same finger to match the force engages similar regions of skin and requires activation of a limited number of muscles. By contrast production of the matching force with the palm of the contralateral hand is more complex and requires the activation of many muscles in the contralateral arm. However, both types of matching produced similar overestimation of the target force. While the matching force must be self-generated for subjects to overestimate the target, it does not matter if the motor action used is complex and uses remote muscles. Furthermore, the amount of overestimation is similar. This may mean that the extra cues are ignored by subjects in favour of matching cues available during both the target presentation and the match. Alternatively, it may mean that any attenuation occurs at high levels when perceptions generated from different signals can be compared.

Previous models describing a force attenuation process (Bays & Wolpert, 2007, Fig. 2*A*) have suggested that the overestimation effect is due to 'attenuation' of the reafferent sensory feedback so that this feedback, which is generated when the subject's own action produces the matching force, is perceived with less weight or importance than the exafference. This seems useful as it sensitises us to external perturbations from the environment, about which we have no other information. However, importantly, such attenuation of reafference cannot be complete. Not only can no forward model predicting sensory reafference of self-generated actions be perfect, but more importantly, a complete subtraction of sensory reafference would leave no afferent source for force proprioception. The constant force offset of the overestimation effect observed in the present study suggests that the attenuation of the sensory reafference is independent of the level of force. Thus, the sensory reafference is attenuated by a constant amount and what is left behind to be perceived is dependent on the level of force applied and this signal is therefore useful for proprioception. An alternative explanation would be that the sensory reafference is subtracted completely and the brain uses another signal for proprioception, but this does not explain the constant component of the overestimation when subjects match an externally generated force with a self-generated one.

Another important implication of the constant component of the overestimation effect is that it implies that a subject would match an external force of 0 N with a self-generated force of 2–3 N. The overestimation has been shown to be present at forces as low as 0.5 N (Shergill *et al.* 2003) but has not been investigated at even lower forces. We would expect a non-linearity to occur as the target force approaches 0 N so that the matching force versus target force relation intersects the origin. However if the constant component of the force overestimation is due to a constant attenuation of the reafferent signal then a self-generated force of up to 3 N would be attenuated and presumably perceived as a zero force because it is unphysiological for a muscle to generate a negative force (or the perception of such a force).

The experimental task can be split into a target and matching phase. The target phase begins with presentation of the target force, continues with its perception and ends with the subject deciding on their matching goal. The matching phase begins with the initial generation of the matching force and continues though perception of that force, and adjustment until the match is achieved. Attenuation of reafference should influence the perception of force in the matching phase. However, when the target phase is performed with a finger held actively in position, in addition to the constant component discussed above, there is a component that depends on the force level. The gradient between the matching and target force increases from 1.0 to about 1.15–1.2, i.e. subjects produce an additional 15–20% increase in force at each target level. While significantly different from unity, these increased gradients do not always differ significantly from conditions where the target phase is performed with a passive finger. Similarly Shergill *et al.* (2003) saw no significant difference between a passive target phase and an active one. However, we consistently found the increased gain when the target phase was active. It persisted when both the target and matching forces were self generated, abolishing the constant component. If the gradient component was part of the same reafferent attenuation as the constant component, then it should also be abolished when the subject generates both the target and matching forces. Our third experiment (Fig. 4, dashed box, filled column) shows this is not the case.

In Experiment 3, the passive and active version of the task were identical during the matching phase. This suggests that the gradient component of the force overestimation occurred during the target phase of the force matching task. In contrast, the model proposed by Bays & Wolpert (2007) to explain the attenuation of reafferent signals puts the attenuation in the matching phase. It may be that the gradient component is completely independent of the constant component (and the reafferent attenuation process proposed by Bays & Wolpert (2007)). When the finger is active during the target phase of the matching task, the force produced by the finger is determined by the external weight, but is controlled through a voluntary motor command. If a subject reacts to the external perturbation of the weight and adjusts his or her motor command to hold it, then as the motor command is adjusted, the exafference due to the external weight should become reafference of the voluntary action holding the weight. If reafference in the target phase is attenuated as in the matching phase then the overestimation would be cancelled out in the same way as when the target force is self generated by the subject. This is not what we observed. Rather we see the preservation of the constant component and the addition of the gradient component. Furthermore if the gradient component is produced in the target phase, it is an accentuation of the force rather than an attenuation. This suggests that there is a difference in the processing of reafference from planned voluntary actions and reactive voluntary actions. Dyhre-Poulsen (1975) observed a similar situation in the detection of vibration on the skin. During ballistic movement of the finger cutaneous sensibility was depressed, but it was enhanced during exploratory movements. During the active target phase, our subjects were instructed to hold their finger in position while a weight was lowered onto it. It makes good sense that the brain would enhance sensation of reafference in this situation rather than attenuate it because the voluntary force has to be matched to an unpredictable external force as it is applied. Further experiments will be needed to determine the physiological mechanism behind the gradient component of force overestimation, but we suggest that it is generated in the target phase and is due to an enhancement of reafference during reactive voluntary tasks.

So far discussion has focused on what happens at forces below ~25% MVC. Previous studies have only examined forces below ~10% MVC. However it is clear that any overestimation when matching an externally applied target force with a self-applied matching force must be limited by the subject's maximal voluntary force, and results in Experiment 4 show that the overestimation seen in earlier experiments is not preserved at high forces. These results are consistent with a previously reported tendency to undershoot high forces during two-arm matching in which both forces are self-generated (Jones & Hunter, 1982). The results from each of our three high-force conditions were different and there may be other effects, in addition to the two overestimation components, at play. Because our task requires remembering the target force for a period of $\leq$2 s, there could be an effect of temporal order occurring at high forces. There is a small effect of temporal order at low forces (Bays *et al.* 2006), but it is unknown if this is the same at high levels of force. However, if a temporal order effect were present, it should occur in each of the conditions in Experiment 4 (Fig. 5). This means that such an effect is not bigger than the 1–2 N reduction in the overestimation that is seen when the highest level of force is compared to the lowest in the *index passive, match contralateral* condition (Fig. 5*A*). In this condition, because the match is made with the larger muscle group of the contralateral arm, the muscles do not approach their maximal voluntary force. When the smaller muscle group, which flexes the index finger, is used in the *index passive, match index-flexion*, there is an underestimation of high forces (Fig. 5*B*). Comparison of these two conditions suggests that in addition to any temporal order effect, there is another process related to the approach of the matching muscle group to its maximum force. In addition, at high forces, when the finger was active during the target phase the *underestimation* produced by matching with the index finger was reduced (Fig. 5*B* and *C*). If the overestimation seen at low forces is preserved but overwhelmed by an independent effect at high forces, then the difference between the passive and active tasks may be explained by the presence of the gradient component.

In summary we have found that subjects overestimate an externally generated target force when matching it with a self-applied voluntary force at low, but not high, levels of force. Furthermore this effect occurs for multiple sensory channels involved in force perception. As well as an offset in the matching force, we report a second novel component that increases the gradient between the matching and target forces. This gradient is consistently present if the target force is received by a finger which is actively holding its position and persists if the constant component is abolished. We suggest that the gain component is generated in the target phase of the matching task and that it is due to an enhancement of the reafferent signals from the voluntary reactive task. Our results do not exclude the presence of a process that attenuates sensory reafference, but they do suggest that the process is more complicated than a simple linear cancellation or attenuation of reafferent sensory signals.

References

Angel RW & Malenka RC (1982). Velocity-dependent suppression of cutaneous sensitivity during movement. *Exp Neurol* **77**, 266–274.

Bays PM, Flanagan JR & Wolpert DM (2006). Attenuation of self-generated tactile sensations is predictive, not postdictive. *PloS Biol* **4**, 281–284.

Bays PM & Wolpert DM (2007). Computational principles of sensorimotor control that minimize uncertainty and variability. *J Physiol* **578**, 387–396.

Blakemore S-J, Wolpert DM & Frith CD (1998). Central cancellation of self-produced tickle sensation. *Nat Neurosci* **1**, 635–640.

Bell CC (1982). Properties of a modifiable efference copy in an electric fish. *J Neurophysiol* **47**, 1043–1056.

Brouwer B, Sale MV & Nordstrom MA (2001). Asymmetry of motor cortex excitability during a simple motor task: relationships with handedness and manual performance. *Exp Brain Res* **138**, 467–476.

Carson R, Riek S & Shahbazpour N (2002). Central and peripheral mediation of human force sensation following eccentric or concentric contractions. *J Physiol* **593**, 913–925.

Coquery J-M (1978). Role of active movement in control of afferent input from skin in cat and man. In *Active Touch*, ed. Gordon G, pp. 161–169. Pergamon, Oxford.

Cullen KE, Brooks JX & Sadeghi SG (2009). How actions alter sensory processing: reafference in the vestibular system. *Ann N Y Acad Sci* **1164**, 29–36.

Dyhre-Poulsen P (1975). Increased vibration threshold before movements in human subjects. *Exp Neurol* **47**, 516–522.

Gandevia SC (1996). Kinesthesia: roles for afferent signals and motor command. In Handbook of Physiology: section 12, *Exercise: Regulation and Integration of Multiple Systems*, ed. Rowell LB & Shepherd JT, pp. 128–172. Oxford University Press, New York.

Gandevia SC & McCloskey DI (1977). Sensations of heaviness. *Brain* **100**, 345–354.

Gandevia SC, Smith JL, Crawford M, Proske U & Taylor JL (2006). Motor commands contribute to human position sense. *J Physiol* **571**, 703–710.

Goodwin GM, McCloskey DI & Matthews PBC (1972). The contribution of muscle afferents to kinæsthesia shown by vibration induced illusion of movement and by the effects of paralysing joint afferents. *Brain* **95**, 705–748.

Jiang W, Chapman CE & Lamarre Y (1990). Modulation of somatosensory evoked responses in the primary somatosensory cortex produced by intracortical microstimulation of the motor cortex in the monkey. *Exp Brain Res* **80**, 333–344.

Jones LA & Hunter IW (1982). Force sensation in isometric contractions: a relative force effect. *Brain Res* **244**, 86–189.

McCloskey DI, Ebeling P & Goodwin GM (1974). Estimation of weights and tensions and apparent involvement of a "sense of effort". *Exp Neurol* **42**, 220–232.

Milne RJ, Aniss AM, Kay NE & Gandevia SC (1988). Reduction in perceived intensity of cutaneous stimuli during movement: a quantitative study. *Exp Brain Res* **70**, 569–576.

Roy JE & Cullen KE (2001). Selective processing of vestibular reafference during self-generated head motion. *J Neurosci* **21**, 2131–2142.

Shergill S, Bays P, Frith C & Wolpert D (2003). Two eyes for and eye: The neuroscience of force escalation. *Science* **301**, 187.

Shergill SS, Gabrielle S, Bays PM, Frith CD & Wolpert DM (2005). Evidence for sensory prediction deficits in schizophrenia. *Am J Psychiatry* **162**, 2384–2386.

Sperry RW (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* **43**, 482–489.

Starr A & Cohen LG (1985). 'Gating' of somatosensory evoked potentials begins before the onset of voluntary movement in man. *Brain Res* **348**, 183–186.

von Holst E (1954). Relations between the central nervous system and the peripheral organs. *Br J Animal Behav* **2**, 89–94.

Voss M, Bays PM, Rothwell JC & Wolpert DM (2007). An improvement in perception of self-generated tactile stimuli following theta-burst stimulation of primary motor cortex. *Neuropsychologia* **45**, 2712–2717.

Walsh LD, Hesse CW, Morgan DL & Proske U (2004). Human forearm position sense after fatigue of elbow flexor muscles. *J Physiol* **558**, 705–715.

Walsh LD, Gandevia SC & Taylor JL (2010). Illusory movements of a phantom hand grade with the duration and magnitude of motor commands. *J Physiol* **588**, 1269–1280.

Walsh LD, Smith JL, Gandevia SC & Taylor JL (2009). The combined effect of muscle contraction history and motor commands on human position sense. *Exp Brain Res* **195**, 603–610.

Weiskrantz L, Elliott J & Darlington C (1971). Preliminary observations on tickling oneself. *Nature* **230**, 598.

Williams SR, Shenasa J & Chapman CE (1998). Time course and magnitude of movement-related gating of tactile detection in humans. I. Importance of stimulus location. *J Neurophysiol* **79**, 947–963.

Author contributions

Each author contributed to all aspects of the study and approved the final version of the manuscript. All experiments were performed at Neuroscience Research Australia (formerly Prince of Wales Medical Research Institute) in Sydney, Australia.

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